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Neurophysiological Correlates of the Behavioral Response to Light in the Sea Anemone *Anthopleura elegantissima*

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Abstract. Neurophysiological responses to light in *Anthopleura elegantissima* do not involve the ectodermal slow system 1 (SS1). Activities in both the endodermal slow system 2 (SS2) and the through conducting nerve net (TCNN) change when the lighting changes, but the response is not consistent. Thus, photoreception in *A. elegantissima* probably occurs in the endoderm because SS2 and the TCNN are involved and SS1 is not. We hypothesize either that the photoreception occurs in sensory cells in a local nerve net, with the information then being transmitted to the muscles, or that the muscles themselves are light sensitive. In either case, the TCNN and SS2 become involved after the transduction, and as a consequence—rather than the cause—of muscular activation. The conducting systems of zooxanthellate specimens have a higher frequency of activity than those of apozooxanthellate individuals.

Introduction

Sea anemones have distinct behavioral responses to light (Fleure and Walton, 1907; Parker, 1918; Batham and Pantin, 1950a, 1954; North, 1956; North and Pantin, 1958; Zahl and McLaughlin, 1959). Pearse (1974a) noted that dark-adapted zooxanthellate specimens of *Anthopleura elegantissima* expand within five to ten minutes after exposure to light. Conversely, *Urticina felina* (=*Tealia crassicornis*), an azooxanthellate anemone, contracts within five minutes after exposure to intense light (Fleure and Walton, 1907).

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Although sea anemones respond to light, no photoreceptor has been identified in these animals. Sensory cells have been described, but definite functions cannot readily be assigned to them (Batham *et al.*, 1960; Fautin and Mariscal, 1991; Shick, 1991). Batham and Pantin (1954) investigated the light response in *Metridium senile* and found that light acted on the parietal musculature in the endoderm. Because the action of light on the muscle was not abolished by magnesium chloride anesthesia (which inhibits myoneural transmission), they concluded that light was acting directly on the muscles in this anemone.

Cnidarians are morphologically the simplest animals to have a nervous system, and in actinarian anthozoans it comprises at least three different conducting systems, one with a conducting velocity 10–20 times faster than those of the other two. The through conducting nerve net (TCNN) has the fastest conducting velocity, up to 100 cm s^{-1}, whereas slow system 1 (SS1) conducts at 5–12 cm s^{-1}, and slow system 2 (SS2) at 3.0–5.3 cm s^{-1} (Josephson, 1966; Robson and Josephson, 1969; McFarlane, 1969, 1982; McFarlane *et al.*, 1988). The TCNN is found in the endoderm of the column and the ectoderm of the oral disc and tentacles. The SS1 is located in the ectoderm, whereas the SS2 is endodermal (McFarlane, 1982; McFarlane *et al.*, 1988).

Using extracellular recordings, Marks (1976) found that the burrowing anemone *Calamactis praelongus* responded to light with a local contraction of the column that was unaccompanied by TCNN activity. Light could also evoke pulses in the TCNN in this anemone, although Marks was not sure whether light acted on the TCNN directly or whether the TCNN was involved in the final processing of the light response. No slow-conducting systems were found in this anemone.

In the present investigation, extracellular recordings were used to evaluate the neurophysiological correlates of the response to a light:dark change in zooxanthellate and apozooxanthellate specimens of *Anthopleura elegantissima* and to provide the first such data on this species. Novel methods of data analysis were developed to allow integration of electrical activity over long time intervals.

Materials and Methods

Zooxanthellate and apozooxanthellate specimens of *A. elegantissima* were collected near Bodega Marine Laboratory, Bodega Bay, California, and shipped to Orono, Maine. Zooxanthellate anemones were maintained at a salinity of 30‰ in a 250-liter aquarium that received indirect natural illumination from a nearby window. This illumination was supplemented with light from a tungsten-halogen lamp (QF-500A) on a 10:14 hour light:dark cycle. Under these conditions, a minimum irradiance of 200 μmol photons m^{-2} s^{-1} was maintained when the lamp was on, as measured with a Li-Cor LI-185B quantum photometer fitted with a model LI-1905B cosine corrected sensor (photosynthetically active radiation, 400–700 nm). Apozooxanthellate anemones were maintained at 30‰ in a 40-liter aquarium in a darkened, temperature-controlled incubator. All water temperatures were 15 ± 2°C. Anemones were maintained in aquaria for no more than six months. All animals were fed previously frozen squid twice weekly and were starved for 48 hours before the experiments.

Electrophysiological recordings were made as follows. Two suction electrodes were placed on tentacles on opposite radii of an experimental anemone. The electrodes were made from 1-ml plastic syringes, each with a silver wire threaded through a hole in the barrel and out through the tip into a polyethylene tube. Metal Luer stubs were avoided because they introduce galvanic artifacts. Electrical stimuli were supplied by a Grass SD9 stimulator applied through a suction electrode attached to a tentacle approximately equidistant from the two recording electrodes. Signals from the recording electrodes were passed to a Grass P15 preamplifier and then to a DC amplifier. The recordings were displayed on a Tektronix 5103N storage oscilloscope and were stored on videotape (Sony Betamax) with a Nakamichi DHP-100 digital audio processor sampling at 44 kHz. For analysis, the data recorded on the videotape were reconverted to an analog signal and redigitized (84 Hz sampling rate) using a Zenith microcomputer with a Metrabyte DASH8 A/D converter driven by FORTRAN software. Illumination (200 μmol photons m^{-2} s^{-1}, measured at 400–700 nm) was provided by a Cole-Parmer low-noise illuminator with a fluorescent bulb. The anemones were maintained in plastic cups at 15 ± 1°C on a flow-through copper base plate cooled with a water circulator (Brinkman RC 6).

Individual preparations in which the through conducting nerve net (TCNN), slow system 1 (SS1), and slow system 2 (SS2) could not clearly be distinguished were not used. Recordings were taken while the animals were in the light (Before Dark, BD), in the dark (D), and then in the light again (After Dark, AD). Individuals in which a continuous recording could not be maintained were not used. All animals had at least a 20-min BD period, a 5-min D period, and a 5-min AD period. Overall, the recordings of five zooxanthellate (specimens S1–S5) and five apozooxanthellate (specimens A1–A5) anemones were analyzed. One of the zooxanthellate anemones (S2) received two dark periods. For this anemone, the intervals consisting of the before-dark, the first dark and the interdark periods are referred to as S2a, whereas the interdark, second dark and afterdark intervals are referred to as S2b.

The pattern of recorded events was analyzed as follows. Only TCNN and SS2 events that occurred on both electrodes simultaneously were scored. Because SS1 activity was very low, this criterion was relaxed, and events that occurred on only one electrode were included as well. These data were then grouped into sets of events per 15-s interval. The 15-s bin was chosen to decrease random variability and to enhance a pattern observed in the data scored per second. The distribution pattern of the data was determined with the Poisson probability distribution, the index of dispersion, the index of clumping, and Green's index (Ludwig and Reynolds, 1988). To determine the effect of light on the burst rate in the three recording periods (BD, D, AD) a Kruskal-Wallis nonparametric one-way ANOVA, Dunn's Multiple Comparison Test (Zar, 1984), and Spearman Rank Correlation (SAS) were performed for each anemone. The overall activity in the zooxanthellate versus apozooxanthellate anemones was compared with an ANOVA (SAS GLM procedure) and Duncan's Multiple Range Test.

Results

The electrical events in the TCNN, SS1, and SS2 of *A. elegantissima* following an electrical stimulus are shown in Figure 1. Bursts in these three conducting systems have similar appearances to those seen in other anthozoans (McFarlane, 1969, 1982; Shelton, 1982; McFarlane *et al.*, 1988).

Most experimental anemones showed some degree of contraction during the D treatment, which is the usual response to darkness in *A. elegantissima*. The burst rates measured during these experiments were tested to determine whether the activity in the different conducting systems was randomly distributed within the BD, D, and AD treatments. In treatments that were of short length, or where there was little activity, the distribution tended to be random. In all cases where the bursting was not

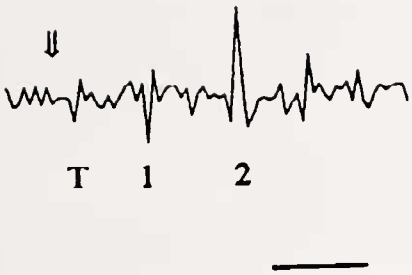

Figure 1. The appearance of activity in the three conducting systems of *Anthopleura elegantissima* after an electrical stimulus given at the arrow. The TCNN is marked by a T, SS1 by a 1, and SS2 by a 2. The scale is 200 ms.

randomly distributed, activity was clumped, as measured by Green's index. There was no apparent relationship between the distribution of the bursts in the conducting systems within the BD, D, and AD treatments and the effect of the light treatment on the burst rates.

The recordings were examined directly so we could determine which conducting system first becomes active after a change in the light treatment. In 6 of 11 cases, a signal from the TCNN was the event first seen when the light was turned off; in the remaining 5 cases an SS2 signal was first (there are 11 dark periods as anemone S2 had two dark periods). In seven cases, a TCNN signal was the first to appear at the beginning of the after-dark period, whereas four cases showed an SS2 pulse first. If an SS2 pulse was seen, it appeared within 2 s of the change in the light condition, but if a TCNN pulse was the first seen, it appeared between 2 and 60 s (and usually closer to 60 s) after the change in the light treatment. SS1 pulses were never seen directly after the light condition changed.

In eight specimens of *A. elegantissima,* a change in burst rate occurred in response to the dark treatment, but the exact effect varied among individuals (Figs. 2–4). Some animals showed an increased burst rate in the dark, whereas others showed a decreased rate. Still other animals had a burst rate in the dark that was different from the BD rate but not the AD rate, and some anemones showed the opposite pattern. Except in the case of anemone A3, to be discussed below, the length of the BD, D, and AD period did not seem to affect the rate changes (Table I). Still, although there is no single obvious trend in the time of occurrence, the rate change was clearly due in some manner to the change in illumination.

All five of the zooxanthellate (S1–S5) and three (A3–A5) of the apozooxanthellate specimens of *A. elegantissima* showed a statistically significant change in burst rate due to changes in illumination (Table II), although the system in which the change was seen varied among individuals. In seven anemones, a significant difference in burst rate within SS2 was attributable to the dark interval

Table I

Duration (min) of the Before Dark, Dark, and After Dark intervals

Anemone #	BD	D	AD	Total (min)
S1	25.00	5.00	5.00	30.00
S2a	31.00	6.00	10.00	47.00
S2b	10.00	5.00	15.26	67.26
S3	30.55	6.00	20.07	57.02
S4	30.31	7.00	9.43	47.14
S5	40.44	5.00	13.25	59.19
A1	31.10	6.00	18.56	57.06
A2	19.02	5.00	24.00	48.02
A3	24.48	20.00	10.00	54.48
A4	22.55	5.00	19.59	47.54
A5	34.00	5.00	20.00	59.03

(Fig. 2); in four of these anemones a significant difference in burst rate occurred within the TCNN as well (Fig. 3). In darkness, one anemone (A3) had a significant change in burst rate in the TCNN only (Fig. 3), and one anemone (S1) had a significant difference in burst rate within SS2, the TCNN, and SS1 (Figs. 2–4). The latter was the only anemone in which a significant change in burst rate due to the darkness was found in the SS1; this anemone had no SS1 bursts in the after-dark period, which may explain this finding. If the recording period in the AD interval had been longer, there would probably have been an SS1 burst, and then there would not have been a significant difference in frequency of activity in SS1. Two apozooxanthellate anemones (A1 and A2) showed no statistically significant changes in burst rates due to changes in illumination.

Anemone A3 showed a significant difference in burst rate only in the TCNN. The rate during the AD period

Table II

Results of the Kruskal-Wallis ANOVA comparing rates of activity in the BD, D, and AD intervals in each of the conducting systems

Anemone #	TCNN	SS2	SS1
S1	21.40†	22.83†	18.37†
S2	43.36†	42.69†	8.35
S3	10.19○	25.58†	2.98
S4	1.69	14.53•	4.76
S5	3.59	6.43*	2.39
A1	1.25	3.30	1.88
A2	0.91	3.70	0.98
A3	13.81•	0.03	4.12
A4	19.98†	10.73○	2.27
A5	1.09	7.72*	4.53

* $P < 0.05$.
○ $P < 0.01$.
• $P < 0.001$.
† $P < 0.0001$.

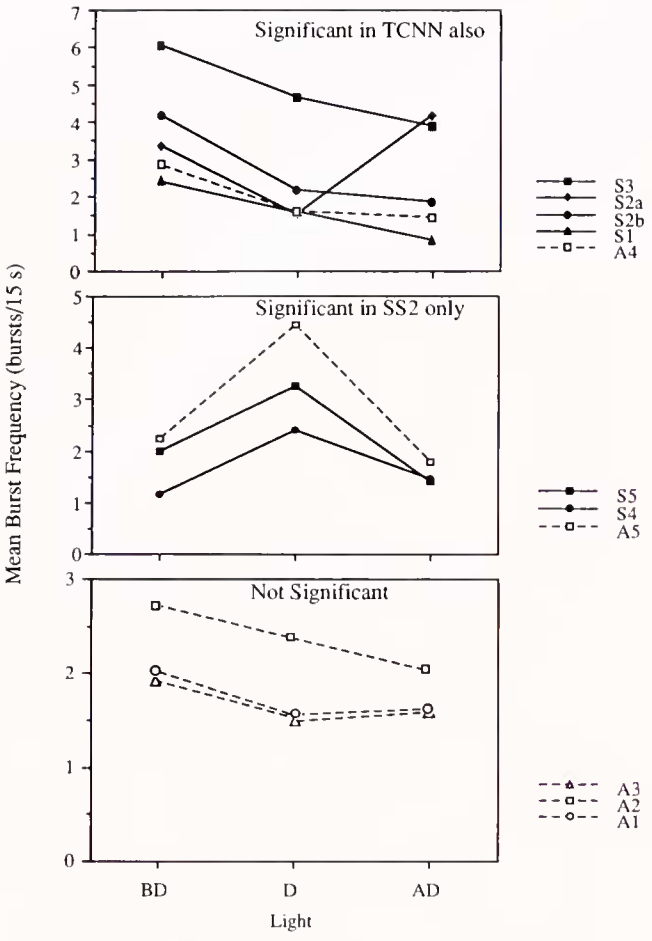

Figure 2. Averages of burst frequency in SS2 of 10 specimens of *Anthopleura elegantissima* during the BD, D, and AD intervals. Anemones are grouped by burst pattern. Those anemones in which there is a significant difference in activity in SS2 and in the TCNN are grouped together in the upper portion of the figure. Anemones in which there is a significant difference in activity only in SS2 are grouped together in the middle portion of the figure. Anemones in which there is no significant difference in activity in SS2 are grouped together in the bottom portion of the figure. Zooxanthellate (S) anemones are indicated by solid lines, and apozooxanthellate (A) anemones are indicated by dashed lines; numbers denote individual specimens. Standard errors are not shown, but range from 5 to 33% of the means.

was significantly lower than those in the BD and D intervals. This anemone had a 20-min dark period, the only dark period longer than 7 min (Table 1). This specimen was the only one to show significance in the TCNN alone. It is interesting that the only anemone having a long dark treatment was the only anemone not to show a significant change in SS2 burst rate resulting from the change in irradiance.

The frequency of activity in the TCNN, SS1, and SS2 is higher in zooxanthellate anemones than in apozooxanthellate individuals ($P < 0.0001$, Duncan's Multiple Range Test). This may be manifested in the greater responsiveness of the zooxanthellate anemones in behavioral studies (unpub. results), and also be related to the greater effect the dark treatment had on the burst rates, because all of the zooxanthellate anemones showed a significant effect of the treatment, whereas only three of the apozooxanthellate anemones did.

The burst rates in the three conducting systems were tested for correlation with each other. Seven anemones (S1, S2, S3, S5, A1, A3, and A4) had activity in the TCNN positively correlated with activity in SS2 ($P < 0.001$). Six anemones (S3, S5, A1, A3, A4, and A5) had activity in the TCNN positively correlated with activity in SS1 ($P < 0.03$), and four anemones (S2, S3, S5, and A1) had SS2 activity positively correlated with activity in SS1 ($P < 0.03$). Anemone A2 was the only one to show no correlation in activity among the conducting systems and no effect of the light treatments on burst rate. One anemone (A1) in which the light treatment did not have an effect

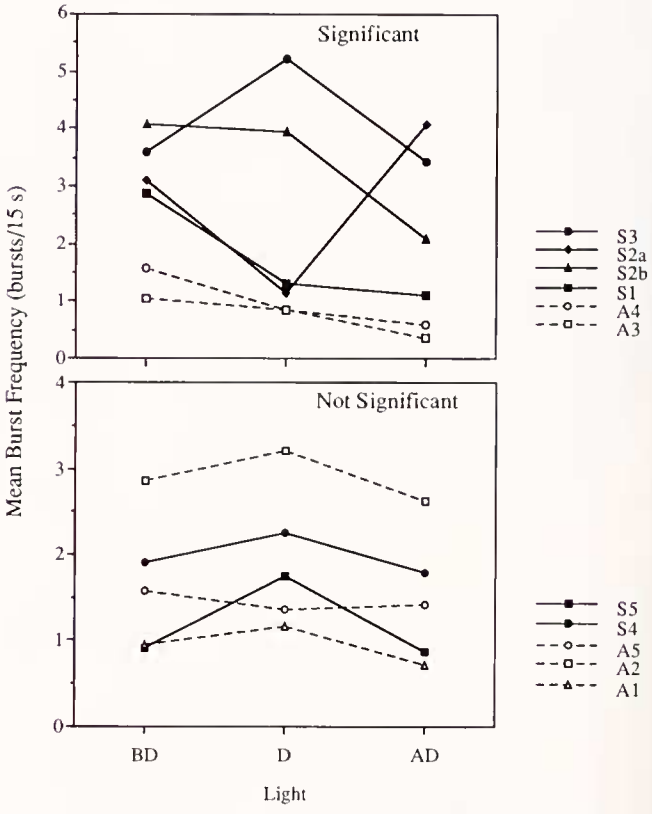

Figure 3. Averages of burst frequency in the TCNN of 10 specimens of *Anthopleura elegantissima* during the BD, D, and AD intervals. Anemones in which there is a significant difference in activity in the TCNN are grouped together in the top portion of the figure, whereas anemones in which there is not a significant difference in activity are grouped together in the bottom portion of the figure. Zooxanthellate (S) anemones are indicated by solid lines, and apozooxanthellate (A) anemones are indicated by dashed lines; numbers denote individual specimens. Standard errors are not shown, but range from less than 1 to 33% of the means.

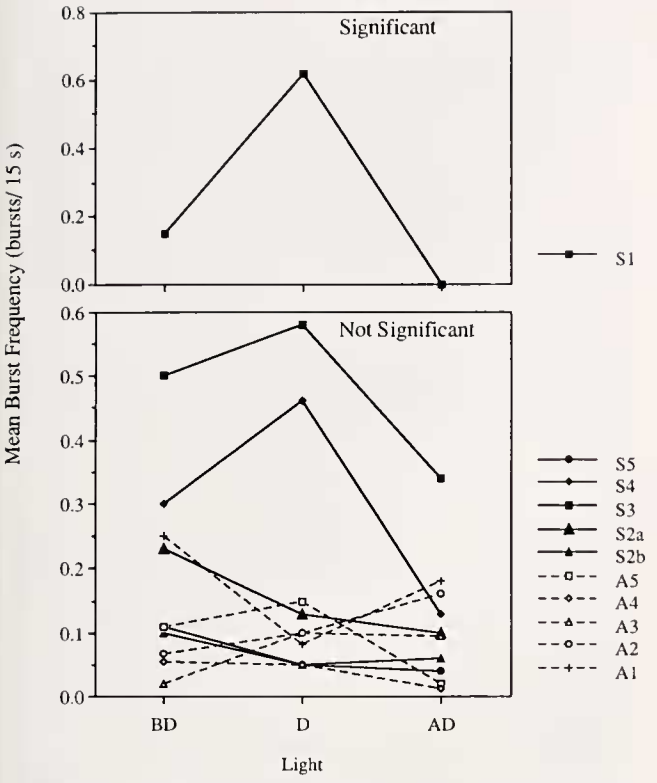

Figure 4. Averages of burst frequency in SS1 of 10 specimens of *Anthopleura elegantissima* during the BD, D, and AD intervals. The anemone in which there is a significant difference in activity in SS1 is shown in the top portion of the figure, whereas anemones in which there is not a significant difference in activity in SS1 are grouped together in the bottom portion of the figure. Zooxanthellate (S) anemones are indicated by solid lines, and apozooxanthellate (A) anemones are indicated by dashed lines; numbers denote individual specimens. Standard errors are not shown, but range from 2 to 100% of the means.

on burst rate did show correlation in activity among all three conducting systems. This anemone (A1) and the anemones S3 and S5 were the only individuals that showed correlation in activity among all the conducting systems.

Discussion

Because we never observed pulses in the ectodermal SS1 of *Anthopleura elegantissima* in response to a light-dark change, our results support the endodermal locus of the light response noted by Batham and Pantin (1950a, 1954) and by Marks (1976) in other species of anemones. McFarlane (1983) noted that SS1 is not spontaneously active in *C. parasitica*. This observation also pertains to *A. elegantissima*, where SS1 pulses were rare (Fig. 4). The number of recorded SS1 pulses may even have been artifactually high owing to the recording method, because some pulses recorded by only one electrode were classified as SS1. Because SS1 is not spontaneously active in *A. elegantissima* and is not activated by a change in irradiance, the ectoderm is probably not the site of photoreception in this sea anemone.

When the change in irradiance causes contraction in the anemones, the conducting systems could be involved in three ways: (1) the frequency of activity would increase in the TCNN and decrease in SS2, because SS2 is inhibitory to TCNN pacemaker activity (McFarlane, 1974a, b, 1983; McFarlane *et al.*, 1988; Pickens, 1988); (2) the frequency of activity in the TCNN could remain constant, while the burst rate in SS2 decreased; (3) SS2 activity could remain constant while TCNN activity increased. Any of these would produce a relative reduction of the inhibitory effects of the SS2.

In *A. elegantissima*, when the illumination changed, there was a change in activity in the TCNN and SS2 in some individuals (Figs. 2, 3). The frequency of activity in the TCNN did not increase when SS2 activity decreased (Figs. 2, 3), which would have been expected if the hypothesis were correct that in some way the light change reduces the inhibitory effects of SS2 on the TCNN. The conducting system responsible for initiating the light response cannot be specified because a change in light sometimes induced a pulse from the TCNN first and sometimes a pulse from SS2 first.

The large individual variation in the response of the conducting system to irradiance changes seems paradoxical. The change in irradiance obviously affected the anemones as they would often contract during the dark period and so pull off the suction electrodes. The recordings presented here may therefore be biased toward less responsive individuals because the data are from anemones that did not contract fully during the dark period.

The response to light itself is also difficult to explain. If a change in activity in the TCNN or SS2 is carrying the information regarding conditions of illumination, then the change in rate of activity should always be in the same direction. This was not the case, suggesting again that the data presented here are of necessity from anemones that did not fully contract, *i.e.*, those that may have perceived the change but failed to respond to it. This would argue that the TCNN and SS2 are not involved in the initial response to light.

In *C. parasitica*, SS2 activity can be triggered by endodermal sensory cells that detect stress between opposing muscle groups; as a muscle field contracts, SS2 activity is enhanced. This would act as a control over contraction (Batham *et al.*, 1960; McFarlane, 1974b). Spontaneous, or inherent, contractions are not always accompanied by activity in the TCNN in *C. parasitica*. These inherent contractions may result from activity in a local nerve net, and it is this local system that may integrate information from the sensory cells (McFarlane, 1974a, b).

Photoreception in *A. elegantissima* may occur in a sensory cell of a local neuronal network. This photoreceptive sensory cell could be directly connected to the muscles responsible for slow contraction. This local neuronal network might be similar to the one revealed by fluorescent antibodies to Antho-RFamide I and II in *C. parasitica* (Grimmelikhuijzen *et al.*, 1989) and by immunogold-labeling of the tentacular nerve plexus in *Anthopleura elegantissima* (Westfall and Grimmelikhuijzen, 1993). Thus light would affect the muscles of sea anemones without initially involving either the TCNN or SS2. Alternatively, the muscles themselves may be directly photosensitive. Batham and Pantin (1954) believed that the parietal muscles of *Metridium senile* were sensitive to light, although these authors were unable completely to separate the muscular response from possible sensory components. Marks (1976) determined that the parietal and circular muscles of *Calamactis praelongus* were locally sensitive to light. With strong stimuli, pacemakers of the nerve net were activated. This is similar to what is proposed for *A. elegantissima*. Light is perceived by sensory cells that are connected to muscles, or the light is perceived by the muscles themselves; if sufficient stimulus reaches the muscles, their tension changes, which subsequently alters the activity of the TCNN or SS2.

The effect of irradiance on the frequency of activity in the conducting systems of *A. elegantissima* may depend on the behavioral state of the anemone. Batham and Pantin (1950a, b) have noted that *Metridium senile* has distinct phases of spontaneous or inherent activity. The anemone's response to an external stimulus may depend on its behavioral phase. McFarlane (1973, 1983) has noted similar behavior in *C. parasitica*. No previous electrophysiological recordings investigating long-term behavioral patterns of *A. elegantissima* have been reported. As in *C. parasitica*, inherent activity in *A. elegantissima* is probably used to maintain body shape, and external stimuli are coded by changes in activity in the relevant conducting system. The direction and degree of change may depend on the prevailing behavioral phase of the anemone and on the strength of the stimulus.

The conducting systems in zooxanthellate specimens of *A. elegantissima* are much more active than those in apozooxanthellate conspecifics (Figs. 2, 3, 4) and also more active than those in azooxanthellate *C. parasitica* (*cf.* McFarlane, 1973). Greater activity in zooxanthellate *A. elegantissima* may reflect the extra sensory information that these animals are receiving from their algal endosymbionts. Electrophysiological responses to, *e.g.*, oxygen were not investigated, but these animals are sensitive to it (Pearse, 1974a, b; Fredericks, 1976; Shick and Brown, 1977). Certainly the internal P_{O_2} of zooxanthellate specimens of *A. elegantissima* can change quickly (Dykens and Shick, 1982). This added stimulation may be reflected in the higher activity levels in the conducting systems of the zooxanthellate specimens.

The electrophysiologically defined conducting systems (SS1, SS2, and TCNN) in sea anemones are responsible for coordinating a variety of behaviors, and each system has several different roles. SS2, for example, helps coordinate the rhythm of expansion and contraction, chemically induced shell climbing, feeding activity involving chemoreception, and tentacle movement (McFarlane and Lawn, 1972; McFarlane, 1974a, b, 1975, 1983; Boothby and McFarlane, 1986). These three conducting systems may be more global (McFarlane, 1984; McFarlane *et al.*, 1988) than the low-level, local systems that respond directly to every sensory input. Rather, these global conducting systems integrate and coordinate behavioral responses resulting from local perception of manifold sensory stimuli.

This investigation differs from other electrophysiological studies on sea anemones in the method of data collection and analysis. Storing the data on magnetic media allowed for a lengthy study of the electrical pulses in the three conducting systems. The statistical analysis of these data was an attempt to reveal the overall pattern of activity in response to a change in irradiance, rather than the minute-to-minute changes, which are highly variable. This is not the first attempt to examine and quantify long-term electrophysiological recordings of sea anemones (see McFarlane, 1973), but the method is more quantitative and may prove useful in future studies.

Acknowledgments

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Literature Cited

Batham, E. J., and C. F. A. Pantin. 1950a. Phases of activity in the sea-anemone, *Metridium senile* (L.), and their relation to external stimuli. *J. Exp. Biol.* **27:** 377–399.

Batham, E. J., and C. F. A. Pantin. 1950b. Inherent activity in the sea-anemone, *Metridium senile*. *J. Exp. Biol.* **27:** 290–301.

Batham, E. J., and C. F. A. Pantin. 1954. Slow contraction and its relation to spontaneous activity in the sea-anemone *Metridium senile* (L.). *J. Exp. Biol.* **31:** 84–103.

Batham, E. J., C. F. A. Pantin, and E. A. Robson. 1960. The nerve-net of the sea-anemone *Metridium senile*: the mesenteries and the column. *Q. J. Microsc. Sci.* **101:** 487–510.

Boothby, K. M., and I. D. McFarlane. 1986. Chemoreception in sea anemones: Betaine stimulates the pre-feeding response in *Urticina eques* and *U. felina*. *J. Exp. Biol.* **125:** 385–389.

Dykens, J. A., and J. M. Shick. 1982. Oxygen production by endosymbiotic algae controls superoxide dismutase in their animal host. *Nature* **297:** 579–580.

Fautin, D. G., and R. N. Mariscal. 1991. Cnidaria: Anthozoa. Pp. 267–358 in *Microscopic Anatomy of Invertebrates Vol. 2. Placozoa, Porifera, Cnidaria, and Ctenophora*, F. W. Harrison and J. A. Westfall, eds. Wiley-Liss, Inc., New York.

Fleure, H. J., and C. L. Walton. 1907. Notes on the habits of some sea anemones. *Zool. Anz.* **31:** 212–220.

Fredericks, C. A. 1976. Oxygen as a limiting factor in phototaxis and in intraclonal spacing of the sea anemone *Anthopleura elegantissima*. *Mar. Biol.* **38:** 25–28.

Grimmelikhuijzen, C. J. P., D. Graff, and I. D. McFarlane. 1989. Neurons and neuropeptides in coelenterates. *Arch. Histol. Cytol.* **52:** 265–278.

Josephson, R. K. 1966. Neuromuscular transmission in a sea anemone. *J. Exp. Biol.* **45:** 305–319.

Ludwig, J. A., and J. F. Reynolds. 1988. *Statistical Ecology: A Primer on Methods and Computing*. John Wiley & Sons, New York. 337 pp.

Marks, P. S. 1976. Nervous control of light responses in the sea anemone, *Calamactis praelongus*. *J. Exp. Biol.* **65:** 85–96.

McFarlane, I. D. 1969. Two slow conducting systems in the sea anemone *Calliactis parasitica*. *J. Exp. Biol.* **51:** 377–385.

McFarlane, I. D. 1973. Spontaneous electrical activity in the sea anemone *Calliactis parasitica*. *J. Exp. Biol.* **58:** 77–90.

McFarlane, I. D. 1974a. Excitatory and inhibitory control of inherent contractions in the sea anemone *Calliactis parasitica*. *J. Exp. Biol.* **60:** 397–422.

McFarlane, I. D. 1974b. Control of the pacemaker system of the nervenet in the sea anemone *Calliactis parasitica*. *J. Exp. Biol.* **61:** 129–143.

McFarlane, I. D. 1975. Control of mouth opening and pharynx protrusion during feeding in the sea anemone *Calliactis parasitica*. *J. Exp. Biol.* **63:** 615–626.

McFarlane, I. D. 1982. *Calliactis parasitica*. Pp. 243–265 in *Electrical Conduction and Behaviour in 'Simple' Invertebrates*, G. A. B. Shelton, ed. Clarendon Press, Oxford.

McFarlane, I. D. 1983. Nerve net pacemakers and phases of behavior in the sea anemone *Calliactis parasitica*. *J. Exp. Biol.* **104:** 231–246.

McFarlane, I. D. 1984. Nerve nets and conducting systems in sea anemones: Two pathways excite tentacle contractions in *Calliactis parasitica*. *J. Exp. Biol.* **108:** 137–149.

McFarlane, I. D., D. Graff, and C. J. P. Grimmelikhuijzen. 1988. Evolution of conducting systems and neurotransmitters in the Anthozoa. Pp. 111–140 in *Evolution of the First Nervous Systems*, P. A. V. Anderson, ed. Plenum Press, New York.

McFarlane, I. D., and I. D. Lawn. 1972. Expansion and contraction of the oral disc in the sea anemone *Tealia felina*. *J. Exp. Biol.* **57:** 633–649.

North, W. J. 1956. Sensitivity to light in the sea anemone *Metridium senile* (L.). II. Studies of reaction time variability and the effects of changes in light intensity and temperature. *J. Gen. Physiol.* **10:** 715–733.

North, W. J., and C. F. A. Pantin. 1958. Sensitivity to light in the sea anemone *Metridium senile* (L.): adaptation and action spectra. *Proc. R. Soc. London, B* **148:** 385–396.

Parker, G. H. 1918. Actinian behavior. *J. Exp. Zool.* **22:** 193–229.

Pearse, V. B. 1974a. Modification of sea anemone behavior by symbiotic zooxanthellae: expansion and contraction. *Biol. Bull.* **147:** 641–651.

Pearse, V. B. 1974b. Modification of sea anemone behavior by symbiotic zooxanthellae: phototaxis. *Biol. Bull.* **147:** 630–640.

Pickens, P. E. 1988. Systems that control the burrowing behavior of a sea anemone. *J. Exp. Biol.* **135:** 133–164.

Robson, E. A., and R. K. Josephson. 1969. Neuromuscular properties of mesenteries from the sea-anemone *Metridium*. *J. Exp. Biol.* **50:** 151–168.

Shelton, G. A. B. 1982. Anthozoa. Pp. 203–242 in *Electrical Conduction and Behaviour in 'Simple' Invertebrates*, G. A. B. Shelton, ed. Clarendon Press, Oxford.

Shick, J. M. 1991. *A Functional Biology of Sea Anemones*. Chapman & Hall, London. 395 pp.

Shick, J. M., and W. I. Brown. 1977. Zooxanthellae-produced oxygen promotes sea anemone expansion and eliminates oxygen debt under environmental hypoxia. *J. Exp. Zool.* **201:** 149–155.

Westfall, J. A., and C. J. P. Grimmelikhuijzen. 1993. Antho-RFamide immunoreactivity in neuronal synaptic and nonsynaptic vesicles of sea anemones. *Biol. Bull.* **185:** 109–114.

Zahl, P. A., and J. A. McLaughlin. 1959. Studies in marine biology. IV. On the role of algal cells in the tissues of marine invertebrates. *J. Protozool.* **6:** 344–352.

Zar, J. H. 1984. *Biostatistical Analysis*. Prentice-Hall, Inc. New Jersey. 718 pp.